ECOLOGY OF *CAREX BLANDA* THROUGHOUT A WOODLAND/GRASSLAND ECOTONE:

A SMALL-SCALE STUDY OF A WOODLAND SPECIES IN HETEREOGENEOUS ENVIRONMENTS

BY

Debra Finch

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Dr. Helen Alexander-Chair

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Dr. Craig Martin

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Dr. Bryan Foster

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The Thesis Committee for Debra Finch certifies

that this is the approved Version of the following thesis:

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Committee:

_____

Dr. Helen M. Alexander*

_____

Dr. Craig Martin

_____

Dr. Bryan Foster

Date Approved: _____4/19/10_____

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ABSTRACT

Research on a species' distribution and demography across an ecotone provides a population ecology perspective to the study of ecotones. This study focused on the small-scale distribution of a woodland sedge species (*Carex blanda*) across the heterogeneous environment of a woodland/grassland ecotone in eastern Kansas, USA. Four methods of study were used: observation of naturally occurring plants; a field experiment that focused on the traits of woodland plants when transplanted in woodland, edge, and grassland habitats; a growth chamber experiment where plants from three habitats (woodland, edge, grassland) were grown in high and low light levels; and a herbarium survey of the habitats in which these plants are found in Kansas. In response to different environments, plants showed phenotypic plasticity in morphology and varied in disease incidence. Plants in high light environments were short, broad, produced more seeds, and had lower incidence of rust and smut diseases; those in low light were tall, narrow, produced less seeds, and had disease incidence. Plants growing in the edge habitat, the environment between the high and low light environments, had a mix of morphologies and traits of the other two habitats. Although this species is primarily reported in woodland habitat in eastern North America, results at this study site suggested populations can also persist in open grasslands.

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INTRODUCTION

Ecotones, described broadly as transition zones between ecological communities, are ubiquitous in nature (Holland 1988; Risser 1995; Lloyd et al. 2000; Ries et al. 2004; Peters et al. 2006). These areas have long intrigued ecologists (Clements 1905; Holland et al. 1991; Fortin et al. 2000), in part because of the relationship between ecotones and species distributional limits. As the distribution structure of an individual species is affected by its response patterns to the biotic and abiotic environments of ecotones, ecotones may limit species distribution or, alternatively, species may expand their distributional range and establish in novel habitats across the ecotone (Pulliam, 2000; Kawecki 2008). Successful plant establishment in new habitats depends on the ability of genotypes to develop appropriate phenotypes for heterogeneous environments. If a species can produce suitable phenotypes for different environments, then the chances are increased for high relative fitness across an ecotone (Schmitt et al. 2003).

The biotic and abiotic features of habitats within and around ecotones are diverse, contributing to complex environmental heterogeneity (Bell et al. 2000; Gehlhausen et al. 2000; Walker et al. 2003). Many current research studies of ecotones focus on species distributions and community vegetation patterns of transitional areas on a large spatial scale (km or ha) (Bell et al. 2000; Tolman, 2006; van Rensburg et al. 2009). While much can be learned from a large-scale community approach, smaller scale studies (10's of meters) of the distribution of an individual species and its responses to environmental variation can offer insights into population-level processes operating across the ecotone (Clough et al. 1979; Emery et al. 1994; Donohue et al 2000; Griffith and Sultan 2004).

With an individual species approach, focus can be given to demographic variables (growth, reproduction, and plant survival) and biotic interactions (disease incidence and resource competition) as traits and processes affected by environmental variation. Emphasis on a single species also facilitates implementation of experimental approaches in both the field and growth chamber.

Specifically, this study examined the responses of the herbaceous perennial *Carex blanda* Dewey (Cyperaceae) to biotic and abiotic conditions of a deciduous woodland/grassland ecotone in order to assess distribution across an ecotone and to explore processes important to persistence. On geographic spatial scales, the woodland/grassland ecotone is a historically major landscape feature in North America due to a precipitation gradient between the forests of the eastern United States and the prairie lands of the Great Plains. This ecotone delineation persists in modern times with nonnative grasslands and crops replacing most native prairie habitat. The common name for *C. blanda* is woodland sedge, and, as its name suggests, the plant is documented in pine and hardwood forests, woodland streambanks, and wood edges throughout the forests of eastern North America and into the forests of the woodland/grassland ecotone of the Great Plains (Bryson 1980; Great Plains Flora Association 1997). *C. blanda* is also reported to occur "rarely in meadows" (Great Plains Flora Association 1997) and has been ascribed a coefficient of conservatism of 1 because of its occurrence in a range of habitats (Freeman and Morse 2002; Jog et al. 2006). While past ecological work on this species focused on an ecotone of large geographical scale (100's of km; Alexander et al. 2007), this study shifted focus to a much smaller scale (1 - 10's of meters), the scale at which individual plants disperse

seeds. The smaller scale ecotone of this study had three habitats (woodland, edge, grassland) occurring in a deciduous woodland area bordering a native open grassland.

I used four approaches to examine *C. blanda* responses to environmental conditions of a woodland/grassland ecotone in the western part of its distribution (eastern Kansas, USA). One, field surveys were performed to determine the distribution of *C. blanda* across an ecotone and to ascertain variation in plant size and biomass allocation among the different habitats of this ecotone. Two, I used a field transplant experiment where woodland *C. blanda* plants were planted into woodland, edge, and grassland habitats to examine responses of plants from one source to three environments. With this experiment, transplanted individuals were positioned in either a competitive or noncompetitive situation, similar to those observed in previous field work (Alexander et al. 2007), to study the effect of intraspecific competition on plant responses and to determine if these responses varied across the three habitats. All plants placed in transplant holes were *C. blanda* individuals to facilitate a focus on intraspecific competition. Survival, size, seed production, and disease incidence measurements were taken from transplanted individuals and, also, from nearby naturally occurring plants. Additionally, light level measurements were taken on experimental plants to quantify the diverse light environments of the habitats. Three, I designed a growth chamber experiment with naturally occurring plants obtained from woodland, edge, and grassland habitats at the field site to examine plant morphology under high and low light intensities. Four, given that the above field work focused on a single site, I conducted a herbarium

survey to obtain a broader geographical perspective on distributional patterns of *C. blanda* in Kansas.

In using these four approaches, the following questions were addressed: 1) Does *C. blanda* occur throughout the heterogeneous environments of a woodland/grassland ecotone? If so, what are the distributional patterns? 2) Do plants from a woodland source when transplanted back into woodland, edge, and grassland habitats respond with variation in survival, size, seed production, and disease incidence? Does intraspecific competition affect plant response? And do naturally occurring plants vary in survival, size, seed production, and disease incidence among habitats? 3) How do plants of three different habitat sources respond when grown under a similar light environment? 4) Are the distributional patterns of the woodland/grassland study site similar to those patterns recorded from a larger geographical survey?

METHODS

Study species and field site

C. blanda individuals vary in size with culms from 10 - 60 cm tall. In Kansas, plants flower in late April through mid-May, producing seeds from mid-May through June (Great Plains Flora Association 1997; Alexander *et al.* 2007). Plants lack extensive clonal growth by rhizomes and are caespitose.

Infection by two fungal pathogens, a smut and a rust fungus, commonly occurs on plants in Kansas (Alexander et al. 2007). The smut fungus, *Anthracoidea blanda* (Vanky and H. Alexander), targets the ovaries of the host plant. The smut teliospores are produced in

sori that supplant the ovaries, rendering infected flowers sterile. The rust pathogen is a member of the *Puccinia caricina* species complex (from ITS sequence comparisons with GenBank; L. Szabo, personal communications) and produces uredospores on the leaves of its host in spring and summer that later develop into teliospores in autumn. Sexual stages of *P. caricina* occur on plants in the Urticaceae and Grossulariaceae (Farr et al. 1989). Common genera in these families include *Ribes* and *Urtica*, which occur throughout Kansas, including the field site used for this study (Great Plains Flora Association 1997).

The study was conducted at and supported by the University of Kansas Field Station, (KUFS), a research unit of the Kansas Biological Survey and the University of Kansas. The field site was located in a woodland/grassland ecotone in northeast Kansas, USA, at the Robinson Tract of the field station, 12 km northeast of Lawrence, Kansas. The site includes 15 hectares of a woodland area that surrounds a 2-hectare grassland (Fig. 1A). The grassland is a native tallgrass prairie site that also has invasion of European grasses and forbs. Long-term management of the grassland site includes controlled burns (four out of seven years prior to this study). The woodland areas are dominated by elm (*Ulmus* spp.), hackberry (*Celtis occidentalis*), Osage orange (*Maclura pomifera*), and honey locust (*Gleditsia triacanthos*) while common species in the grassland site include big bluestem (*Andropogon gerardii),* smooth brome (*Bromus inermis),* and purpletop tridens *(Tridens flavus)*. A transition zone or edge area lies between the grassland and woodland areas. Near the woodland, the edge habitat includes smaller, less dense trees and shrubs, while near the grassland, the edge habitat is dominated by grasses and forbs (Fig. 1, 2).

For my study, I defined the edge area as a strip approximately 8 meters wide based on the heterogeneous vegetation structure and the extent of shading by trees. Plants of *C. blanda* had been known to occur in the wooded areas at the site (H. Alexander, personal communications); the unexpected observation of *C. blanda* in the grassland areas led to this study.

Field survey: Distribution across habitats

Experimental site survey

On May 30, 2006, I determined the density of naturally occurring *C. blanda* plants in the woodland, edge, and grassland areas at the site where the field experiment (see below) was later conducted. I established three 30 m parallel lines, 10 m apart, so that they passed through the three habitat areas (Fig. 1B). In 2 m x 1 m plots along each line, a count was taken of the number of *C. blanda* plants.

Broad survey

On May 19-20, 2007, a broad survey was performed to quantify the distribution of *C. blanda* across the entire study site. I laid three circular transects for sampling, one in each habitat area, grassland (366 m), edge (650 m), and woods (752 m) (Fig. 1A). Transects were established by walking in a circular pattern concentric to the circumference of the grassland habitat. Approximately every 14 meters along the transect in the grassland and every 28 meters in edge and woodland habitats, I placed a 1 m x .5 m rectangular frame on the ground and took a count of *C. blanda* plants within the frame. With this approach, I obtained data for 36, 32, and 37 locations in the grassland,

edge, and woods, respectively. For the plant located nearest the left bottom corner of the frame, I measured plant height (cm, length of longest leaf from base to point) and basal width (mm, at base level with calipers). Basal width measurements were converted to basal area, a variable typically used to measure plant size for species with graminoid morphologies (Malmstrom et al. 2005; Alexander et al. 2007). These methods for measuring plant size were also used in the experimental studies described below.

Field transplant experiment and survey: Plant traits and disease incidence

Overview of field transplant experiment

Given that *C. blanda* occurs primarily in woodland habitat (Bryson 1980; Alexander et al. 2007), I designed a field experiment to investigate response differences in survival, size, achene (= seed) production, and disease incidence of plants of woodland origin when transplanted into grassland, edge, and woodland habitats. Vegetatively divided plants from two northeastern Kansas woodland field sites were available from a previous study (Alexander unpublished) and were used as sources of plants for this study (see details below). Plants from each source were randomly sorted into three groups for placement into three habitats. Given the variation in plant spacing observed at the field site and, more generally, across Kansas (Alexander et al. 2007), plants were arranged in one of two competitive situations during transplanting: noncompetitive with only one plant (target plant) placed in a hole, or competitive with four plants (one target plant surrounded by three neighbor plants) placed together in a hole (Fig. 1C).

Detailed methods

Plant sources and field preparation In the fall of 2005, 26 plants were taken from two woodland sites in northeastern Kansas and were placed in the University of Kansas greenhouse. Site 1 is located on the Briedenthal Reserve, 23 km south of the Robinson site, while Site 2 is located on private land 16 km west of the Robinson site. Fourteen plants (half from Site 1, half from Site 2) were cloned in successive rounds by vegetative division to obtain a total of 168 target plants. The other 12 plants (7 from Site 1, 5 from Site 2) were used as neighbor plants (placed around each target plant). These plants were also cloned in successive rounds by vegetative division to produce a total of 252 neighbor plants.

All plants were kept in the greenhouse under similar environmental conditions until transplanting took place. On June 5-13, 2006, I recorded height and basal width measurements on each plant prior to transplanting. A colored wire was loosely wrapped around the base of each plant to facilitate identification in the field.

To prepare the field transplant experiment site, 30 m parallel transects were established in the woodland, edge, and grassland habitats (Fig. 1B). Two rows of holes were dug along each transect; holes were 9 cm wide x 9 cm deep and were .90 m apart. There were a total of 56 holes (28 in each row) in each habitat. Each row of 28 was in turn divided in half, so that there were 28 plants arranged in the top (i.e., higher on the slight hill) region of each habitat and 28 were arranged in the bottom region (i.e., lower on the slight hill). Finally, for the 56 holes in each habitat, the experimental design incorporated 28 target

plants planted alone (noncompetitive; 14 in the top and 14 in the bottom regions) and 28 target plants planted each with three neighbors (competitive; 14 in the top and 14 in the bottom regions) in each habitat (Fig. 1C). A random sampling scheme was used to select plants for placement in holes in the top and bottom regions of transects. On June 14-16, 2006, 420 plants (targets + neighbors) were transplanted into woodland, edge, and grassland habitats at the site. To promote establishment in the field, plants were watered every three to four days for two weeks.

Plant traits Survival data were taken on November 4-5, 2006 (survival from June 2006) and on May 5-12, 2007 (survival from November 2006). For all surviving plants, measurements of plant height and basal width were made on November 4-5, 2006, and May 5-12, 2007. Data collection in the experiment was terminated after October 2007 disease surveys (see below). However, in 2008, above- and belowground plant biomass measurements of surviving plants were used to determine if there were carbon allocation differences of plants from different habitat areas. For biomass measurements, 48 experimental plants were dug up from the field site on June 3, 2008. The objective was to remove 20 randomly selected plants from each habitat; however, one grassland plant was lost in processing and, due to low survival from 2007-2008, only nine woodland plants were removed. Plants were dug from the ground with a shovel and placed in containers for transport to the greenhouse. Roots were gently washed with a garden hose to remove the soil, then plants were placed on racks and air-dried for five weeks. At that time, above- and belowground biomass of each plant was cut apart, both types of biomass

were placed in paper bags, and samples were dried in an oven for eight hours at 76.7° C. Biomass weight measurements were taken after oven-drying was complete.

A seed count was performed on May 21-23, 2007. Seed count per plant was used as an indicator of reproductive output. Number of culms per plant was multiplied by mean seed count from three randomly selected culms to estimate seed production per plant. Presence/absence of smut was recorded on May 21-23, 2007, and of rust on October 28 and November 4-5, 2006, and October 21-28, 2007.

Light levels. To quantify the variation in light levels among and within habitats, I took light measurements at three different times (8:30 am, 12:25 pm and 4:15 pm) on June 24, 2007, using a LI-COR light meter (LI-COR Inc., Lincoln, NE, USA). Five light measurements (N, S, E, W, and directly toward the sun, measured in μmol m^{-2} s^{-1}) were taken at three locations within each habitat. Data for each location is the average of values taken on five experimental plants (the groups of five plants were chosen based on physical proximity and shared light environment).

Field survey: Naturally occurring plants at the experimental site

On May 20, 2007, I labeled 28 naturally occurring plants in the 1-meter border surrounding each experimental transect of the habitats (Fig. 1B). Data on survival, plant size, seed production, and disease incidence was recorded in a similar fashion as for experimental plants. The labeled plants were randomly selected from the populations present (only 28 plants were located in the grassland habitat, so all were studied).

Survival data were recorded on October 21, 2007 (survival from May 20, 2007) and on June 2, 2008 (survival from October 21, 2007). Height and basal width were measured for all plants on May 20, 2007, and for all surviving plants on October 21, 2007, and June 2, 2008. On June 3, 2008, 28 naturally occurring plants were taken from the field site for the purpose of measuring above- and belowground biomass as previously described. The intent was to retrieve ten randomly chosen plants each from the woodland, edge, and grassland transects established in May 2007. However, due to low survival rates in the edge area, only eight plants could be extracted from that habitat.

On May 20, 2007, and June 2, 2008, reproductive output was measured in the manner described above. Presence/absence of smut incidence was recorded on May 21-23, 2007, and of rust on October 21-28, 2007.

Growth chamber study: Effect of light on plant traits

To explore the effect of light intensity on plant morphology, I collected seven naturally occurring plants from each of the three habitats at the field site (woodland, edge, grassland) on June 16, 2006. Height and basal width measurements were taken from each individual as described above and plants were placed in the greenhouse for eight months. In February 2007, I cloned the viable plants by vegetative division. The goal was to divide each original plant in two so that two light treatment groups of 21 plants would result, with a representative of each plant for each group. This goal was achieved for the edge and grassland plants. However, partly due to the smaller size of the woodland plants, only three of the original woodland plants could be divided in half to

provide a clone for both light treatments. For the other plants, the original plant was placed randomly in one light treatment or the other.

In April 2007, plants were transferred to a growth chamber and placed under one of two light intensities, high light or low light. Light in the high light treatment averaged a photosynthetic photon flux density (PPFD) of 500 μmol m^{-2} s^{-1} and in the low light treatment a PPFD of 50 μmol m^{-2} s^{-1} (LI-COR Inc., Lincoln, NE, USA) during a 12-hour photoperiod. Day/night air temperatures were maintained at 27°/20° C. In October 2007, I recorded survival and took height and basal width measurements using previously discussed methods.

Herbarium survey: Distribution across habitats

I conducted a herbarium survey of *C. blanda* specimens to evaluate how commonly the plant is recorded as growing in open (non-woodland) habitat in Kansas. The R. L. McGregor Herbarium at University of Kansas houses 185 *C. blanda* specimens collected from Kansas. Using the collector's notation, specimens were categorized as collected from forest/woodland, edge/border, grassland/open habitat, or uninformative (either no description or description lacked specifics). For size data, I used plant height (following methods described earlier) as this variable is unlikely to be altered by the process of collecting or mounting a specimen. Basal width measurements were not taken because collectors often divide a large plant into smaller portions that fit on a herbarium sheet (Alexander *et al.* 2007, C. Morse, personal communications).

DATA ANALYSES

All statistical analyses were done in Minitab 15 (Minitab, Inc., State College, PA, USA). For summary statistics, SE is given as a measure of variability. For naturally occurring plants, size and seed count were analyzed with general linear models with habitat as an independent variable. Basal area and mean seed count were log-transformed to correct for heterogeneity in variance.

For experimental plants, size and seed count were analyzed with complex general linear models. Independent variables included habitat, plant source, and competitive arrangement. Additional explanatory variables considered were original plant size and location of an experimental plant in either the top or bottom half of transects (transects started at the bottom of a slope and ran to the top). Analyses were run with all combinations of the focal variables of the experiment (habitat, plant source, competitive arrangement) and additional explanatory variables (original plant size and top/bottom placement). Full models were run first and non-significant terms were eliminated in subsequent model runs. Independent variables were only eliminated if their interaction was not significant. For survival and disease incidence data in both surveys and experiments, chi-square and binary logistic regression analyses were used.

RESULTS

Field survey: Distribution across habitats

Question 1) Does C. blanda occur throughout the heterogeneous environments of a woodland/grassland ecotone? If so, what are the distributional patterns?

In the experimental site survey, plant density varied among habitats with number of plants in the edge habitat higher than in the woodland and grassland areas (Fig. 2). There were significant differences in density among habitats (quadrat counts were averaged over each habitat type per line; $F_{(2,6)} = 24.69$; $p = 0.001$; $R^2 = 89.17\%$).

In the broad survey, *C. blanda* plants were found throughout the woodland, edge, and grassland areas. Although edge habitats had a larger percentage of locations with *C. blanda* plants and higher density at occupied sites, the habitat effect was only marginally significant (Table 1A).

Field transplant experiment and survey: Plant traits and disease incidence

Question 2) Do plants from a woodland source when transplanted back into woodland, edge, and grassland habitats respond with variation in survival, size, seed production, and disease incidence? Does intraspecific competition affect plant response? And do naturally occurring plants vary in survival, size, seed production, and disease incidence among habitats?

Experimental plants

Habitat Survival of experimental plants was uniformally high (>85% through May 2007), with no significant differences in survival among habitats. However, the habitat into which plants were transplanted had a significant effect on plant size. Mean heights for plants placed in the woods were consistently greater than for plants put in edge or

grassland regardless of date measured (Table 2). Edge plants had the highest mean basal area values in both 2006 and 2007 with significant habitat effect in 2006 (Table 2). Woodland means were lowest and habitat effect was significant for both above- and belowground biomass measurements (Table 2).

Although no significant difference among habitats emerged in the percentage of plants that reproduced in May 2007 (woodland 90%; edge 98%; grassland 100%), habitat had a significant effect on seed count with mean grassland seed count 15% greater than edge and 72% greater than woodland means (Table 2).

There were significant differences among habitats in smut incidence with no disease seen on grassland plants (Table 3). For rust presence, habitat effects were significant, with grassland plants incurring the lowest rates of incidence (Table 3).

Competition Target plants without neighbors had higher survival than with neighbors (96 - 98% vs. 89%, depending on time period, $p < 0.05$). Competitive effect was not statistically significant for height. Plants without neighbors had significantly greater mean basal area and seed count (Table 2). Higher rust incidence occurred on plants growing in competitive situations in 2006, but there were no significant differences in rust and smut incidence between the treatments in 2007 (Table 3).

Source For most traits, no effect of plant source was seen. However, Site 2 plants produced more seeds (see Appendix for details). Note that statistical analyses of clonal

variation within the Site 1 and Site 2 source material was not possible due to the very low replication for any one clone within the habitat and competition treatments.

Other factors Placement in the field (top or bottom regions) had few effects (Appendix). For nearly all analyses, there was a significant effect of initial height or basal area, showing that larger size at transplanting did affect later sizes (Appendix). Nearly all interaction terms were not significant; the Appendix includes the few exceptions to this statement.

Light levels Analyses of light measurements taken directly at the sun showed a significant effect of time, habitat, and a time/habitat interaction (Table 4A). Compared to other time periods, morning light measurements were low for all habitats. Among the three habitats, woodland light measurements were low regardless of time of day, while grassland measurements were high in the morning and midday with edge high in the afternoon (Fig. 3). Three-way ANOVA analyses on light measurements taken at the four compass directions (N, S, E, W) showed a significant three-way interaction with time, habitat, and direction. Subsequently, three different two-way ANOVAs were performed, one for each habitat, to better understand the effect of factors. For the woodland habitat, only time of day was significant (Table 4B), with midday light measurements higher than morning and afternoon (Fig. 4). For the two-way ANOVAs of edge and grassland habitats, there were significant effects of time, direction, and the time/direction interaction (Table 4B). In edge habitat, afternoon light measurements were higher than other times, especially when the light meter was pointed to the west. Grassland light

measurements were high in both midday and afternoon, with variation dependent on the compass direction (Fig. 4).

Naturally occurring plants

Habitat The morphology of plants in the three habitats was significantly different for nearly all comparisons (Table 1B). Mean heights of naturally occurring woodland plants were consistently greater than those for edge and grassland plants in the border survey of 2007 and 2008. For basal area, grassland plant means were greater than woodland and edge plants for all surveys and dates. Although differences were only marginally significant ($.05<p<0.1$), aboveground biomass mean values for woodland plants were larger than means for other habitats, while belowground biomass mean values for grassland plants were greatest.

Nearly all plants reproduced in 2007 and 2008 (Table 1B). For reproducing plants, patterns in seed production among the habitats depended on survey date. In May 2007, mean seed count for edge plants was highest (102.2), woodland lowest (44.04), and habitat effect was statistically significant ($p=.049$) (Table 1B). However, significant differences in seed production were not found in June 2008, perhaps due to the low sample sizes of edge plants as a result of high mortality between October 2007 and June 2008 (Table 1B).

Smut and rust disease incidence rates were highest for woodland plants (significant effects of habitat, Table 3). Grassland habitat had the least rust incidence; no smut incidence was observed on grassland plants.

Growth chamber study: Effects of light

Question 3) How do plants of three different habitat sources, grown under a similar light environment, respond to their new environment?

Initial size Similar to the survey results, woodland plants collected from the field were, on average, tallest and grassland plants had the largest basal area. Height differences were statistically significant and basal area differences approached significance (Table 5).

Final size After seven months in the light treatments, plants collected from the three habitats did not differ significantly in either mean height for high light treatment or basal area for either of the light treatments (Table 5, Fig. 5). For each clone, plant height was greater for plants placed in low vs. high light treatments, while the opposite was true for basal area.

Herbarium survey: Distribution across habitats

Question 4) Are the distributional patterns of the woodland/grassland study site similar to those patterns recorded from a larger geographical survey?

Of the 185 herbarium specimens, habitat could be assigned for 139 specimens; of these, 86% were from the forest/woodland category with 4% from the edge and 10% from open habitats. As seen in the Robinson tract studies, height of woodland specimens was, on average, taller than edge and grassland specimens, although these differences were not

statistically significant (woodland: 24.5 cm, SE=0.734, n=120; edge: 20.67 cm, SE=4.54, n=6; grassland: 20.92 cm, SE=2.33, n=13; $F_{2,136}$=1.64; p=0.198; R^2=2.35%).

DISCUSSION

Species vary in their distributional patterns across an ecotone. Some species are specific to a habitat, some occur in the ecotone or transitional area separating different habitats, and others are generalists found throughout adjoining habitats and transitional areas. At the 10–100 m spatial scale of this study, *C. blanda* occurs across distinct ecotonal habitats, including woodland, edge, and open grassland sites. These findings are in accord with the coefficient of conservatism classification of 1 ascribed to *C. blanda,* where coefficients of 1-3 describe plants that occur in a variety of habitats (Freeman and Morse 2002, Jog et al. 2006). However, it must be noted that although the floristic study of Jog et al. (2006) found *C. blanda* present in some pastures and meadows, the species was found in only a small percentage of the open habitats sampled. Published accounts of the species (Bryson 1980; Great Plains Flora Association 1997), past research conducted across Kansas (Alexander et al. 2007), and the herbarium survey of this study concur that the distributional range of *C. blanda* is one predominantly contained within woodland habitats. In the herbarium survey, plants were found in both open and woodland habitats, but much more frequently in the wooded habitats. Collector bias is always possible with herbarium studies, but the direction is not obvious (i.e., a collector seeking *C. blanda* might oversample woodland habitats, yet collection might also be more likely for unexpected discoveries of the plant in more open habitats).

Closer examination of the microenvironments where *C. blanda* plants are found may provide insight into patterns of the species' spatial distribution. Although *C. blanda* occurs in low light environments of woodland understories, it also can be found in areas receiving higher light intensity. Plants are commonly found along woodland trails and in understory patches below canopy breaks (Alexander et al. 2007) where sun flecks may occur at high frequency or high duration. The patterns of occurrence and abundance of *C. blanda* across this heterogeneous landscape are likely determined by a variety of processes, including a high level of morphological and physiological plasticity, differential patterns of disease, seed dispersal patterns, and site history.

Phenotypic plasticity

Phenotypic plasticity is increasingly recognized as a ubiquitous and vital source of variation that enables one genotype to produce multiple phenotypes in response to environmental conditions (Sultan 2004, Miner et al. 2005, Galloway and Etterson 2009). Generally, plants occurring in more heterogeneous environments respond with a higher level of phenotypic plasticity than plants in more homogeneous habitats (Emery et al. 1994). Phenotypic plasticity responses are stimulated by environmental cues such as resource limits and changing conditions (Griffith and Sultan 2004). Light, a common resource limitation, is a likely candidate as a cue for morphological responses of *C. blanda.* Increased leaf length in low light environments (likely an etiolation response) and shorter length in high light environments indicated phenotypic plasticity of clones. This study included a growth chamber approach where plants from three habitats were grown in a similar light environment. Plants entered the chamber with different size

measurements responsive to their original habitat and, for plants in the same light treatment, they exited with similar sizes. Thus, within each light environment in the chamber, clones attained similar leaf length and basal area measurements regardless of whether they were originally from woodland, edge, or open area habitats. Plasticity is further demonstrated by the field experiment. Plants had similar size measurements when first placed in the field, but plant size measurements diverged among habitats by the end of the study. The phenotypic plasticity of *C. blanda* demonstrated in these two experimental approaches facilitates its growth under varied light environments. As a result, the species can opportunistically grow across the habitats of this ecotone.

At the field site, light levels in the three habitats were distinctly different. Woodland light levels were generally low, although there is heterogeneity due to breaks in the canopy and sun flecks. Edge light levels were lower in the morning when vegetation from the woodlands filtered sunlight (from the east) and high in the afternoon when the sun had moved past the woodlands canopy and incoming light could more directly strike the edge plants from the west. Grassland light levels were low in the morning when the sun was behind the woodlands vegetation and high at both midday and in the afternoon when plants received full sun. Such distinct differences among habitats may, however, not be maintained throughout the growing season if, for example, taller herbaceous plants shade *C. blanda* plants in the grassland or light differences vary seasonally. By conducting a field transplant experiment in addition to the growth chamber study, plant traits were evaluated under realistic light conditions and exposed to other biotic and abiotic variables (Miner et al. 2005).

Plants responded differently depending on their competitive environment: target plants without neighbors had broader basal area and larger seed counts. However, no habitat x competition interactions emerged from the analyses, revealing that release from intraspecific competition had a consistent effect across habitats. Similarly, there were few significant differences among the plants from the two different woodland sources, suggesting that the morphological changes observed were a general result for this species.

Given the common occurrence of the species in woodland habitats (and its name, woodland sedge), a striking result of this study is that plants growing in woodland habitats did not have the largest biomass or the highest seed production in either field surveys or experiments. Instead, grassland area plants had the largest total biomass of all three habitats. Higher seed counts for grassland plants may be due to the increased size of belowground biomass and basal area at higher light levels, giving these larger plants the capacity for greater water and nutrition acquisition for support of reproductive growth. These data raise the question of the type of photosynthetic pathway used by this species. Both C_3 and C_4 pathways are reported in the Cyperaceae (Teeri et al. 1980; Li et al. 1999), but the photosynthetic pathway of *C. blanda* is not known. If *C. blanda* is C_4, its larger size and seed production in high light environments is not surprising. Measurements of light compensation points and net photosynthetic rates would be needed to better understand the physiological mechanisms behind the response of this species to different light environments (Larcher 2001).

Edge habitat data showed height measurements intermediate in comparison to the woodland and grassland areas. However, basal area and seed count were at different times smallest, largest, and intermediate. One explanation for the mixed results for the edge may be the complex nature of the habitat, with changes in both vegetation structure and shading. It is intriguing, for example, that broad surveys reveal that plant density was often higher in the edge habitat than in the woodland and grassland areas (Table 1A). Similarly, the experimental site survey showed a higher density of plants occurring in the edge habitat with a higher density at the grassland side of the edge habitat than the woodland side (Fig. 2, E1 and E2). A possible explanation for the density difference within the edge habitat could be the variable shade line that changed from morning to afternoon on the grassland edge side if, for example, a heterogeneous light environment of low and high light is favorable for *C. blanda.* It should be noted that size and disease measurements of edge plants, both experimental and naturally occurring, were located on the woodland side of the edge and thus likely had more woodland-like vegetation and light. Measurements on plants at different locations within the edge would be an interesting extension of this study to explore the complexity of the edge environment as it changes from woodland to grassland vegetation and light.

Disease patterns

Grassland plants had less fungal disease than woodland plants: incidence of both *A. blanda* and *P. caricina* pathogens was three times higher in woodland habitats compared to grassland areas. Of the two pathogens, the disparity in rust occurrence among habitats is more likely to contribute to the difference in seed count seen between woodland and

grassland areas. Decreased photosynthesis on a whole plant scale has been linked to incidence of rust infection as well as reduced whole plant dry weight, specifically with partitioning to roots (Paul and Ayres 1984, 1987; Inglese and Paul 2006). As a result, rust infections commonly result in lower seed count of infected plants. Differences in smut incidence are unlikely to explain disparity in seed production between these two habitats. Although smut disease can reduce seed production, often less than 5% of the ovaries on a single plant in this study showed disease symptoms.

It is not surprising that differences in disease incidence were seen among habitats. Disease development is commonly recognized as extensively influenced by environmental variables (Jarosz and Burdon 1988; Mitchell, et al. 2003; Han et al. 2008). In a study of powdery mildew infection of an experimental *Phlox* population, for example, infection was three to five times greater for plants in shaded than exposed populations (Jarosz and Levy 1988). The *C. blanda* populations of this study may have experienced a disease incidence differential due to drier conditions in the grassland habitat (due to higher light and less dense vegetation) and a more humid environment in the woodlands. Humid conditions cause leaves and other plant structures to remain wet for longer periods of time, creating a favorable environment for pathogen growth. Additionally, the presence in the woods of alternate host plants for the rust *P. caricina* may also have contributed to high rust disease in this habitat. Sexual stages of this rust occur on *Ribes* and *Urtica* species, species that are abundant in wooded areas of Kansas such as the study site and are often found in close proximity to *C. blanda* woodland plants. Transfer of the rust to *C. blanda* study plants for the nonsexual stages of its life

cycle would, therefore, have easily been accomplished. Future studies that experimentally manipulate fungal presence/absence through either field inoculation or fungicide studies would be useful for explicitly testing habitat effect on disease incidence and the degree to which disease affects seed production patterns.

Seed dispersal and site history

Prevalence of *C. blanda* in Kansas woodlands (Alexander et al. 2007; herbarium data) and, more generally, in deciduous forests in eastern North America supports the observation that new populations of *C. blanda* in open areas may have originally occurred following dispersal of seeds from woodland plants. However, it appears unlikely that the persistence of open area populations at this site is currently dependent on dispersal from woodlands. Seed production per plant, for example, is lower in woodland populations than either open or edge populations and survival rates for the three habitats were similar. Grassland populations at the site are thus likely to be self-sustaining and even possibly source populations, if more seeds are produced in the grassland than are required for persistence. In source-sink dynamics, seed dispersal from a productive source population may allow a less productive sink population to persist (Keddy 1982; Pulliam 1988). The success of the open area sedge population is also probably affected by the management history at the site. The open grassland area containing the study site was burned four out of the past seven years, so *C. blanda* plants appear to be able to regrow or reestablish from seed in a high light, open area after burning.

A key question is whether seed dispersal plays a major role in the distribution of *C. blanda* across habitats. Seed dispersal mechanisms for *C. blanda,* are, however, not

known. Studies of other forest *Carex* species have found evidence for two seed dispersal methods, "gravity dispersed" (i.e., no specialized dispersal, with little seed movement from the parent plant) or myrmecochory (ant dispersal) (Handel 1976; Vellend et al. 2000), but similar studies for *C. blanda* have not been done.

Future directions

It is challenging to know whether this field site represents a unique situation for *C. blanda* occurrence since distribution studies are rarely studied in as fine detail as done in this study. Further research on *C. blanda* conducted at multiple sites would help examine the possible generality of these findings. For example, it would be interesting to explore whether larger plant size, greater seed production, and reduced disease incidence are common patterns for this woodland species in other grassland sites in Kansas.

In a dynamic area such as an ecotone where species may be pushed to the limits of their tolerance, a high sensitivity to environmental change may be observed (Fortin et al. 2000). Studies of populations growing in ecotonal areas or at the distributional limits of species are of interest because of their place at the front line of climate-induced environmental change, yet little understanding exists regarding relative performance and adaptive potential under different climate conditions (Pearson et al. 2009). Environmental conditions place controls on species distributions by either their interaction with species' physiological tolerance limits or by biotic constraints that change along environmental gradients (Vellend et al. 2000). Future work should take a two-pronged approach to better understand plant response. Specifically, for *C. blanda*

and other species in ecotones, it would be advantageous to take a more explicit physiological approach as well as examine the influence of maternal effects and genetic variation in plant response to environmental heterogeneity. For instance, extension of research on phytochrome-mediated responses to light and its effects on phenotypic plasticity (Schmitt et al. 2003) and studies of plastic responses to canopy shade over more than one plant generation (Galloway and Etterson 2009) would provide important insights.

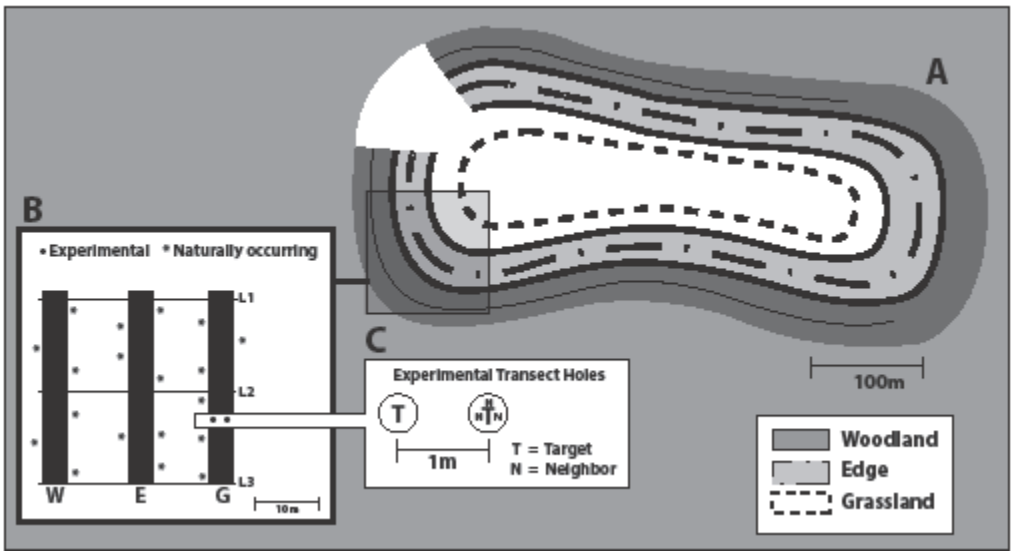


Figure 1. Schematic of field site. A. View of larger area where field transplant experiment site (shaded box) was located. Broad survey lines are located in the three habitats. Broad survey lines were not taken in the upper left area of the diagram, where the grassland habitat expanded into a large field, nor taken in the far right area of the diagram, where boundary fencing prevented woodland surveys from being performed. B. Enlargement of field transplant experiment site. Parallel vertical black bars in habitats (W = woodland, E = edge, G = grassland) represent transect lines where woodland plants were transplanted into 9 cm diameter holes (two rows of 28 holes in each habitat). The asterisks illustrate locations of a subset of the naturally occurring plants (28 total plants per habitat) found in a 1 m border around the experimental transects. The three thin horizontal lines depict the location of the experimental site survey to quantify plant density at the site (see also Figure 2). C. Close-up view of the two types of plantings in the 9 cm holes: Alone (T = target plant only); Competitive (T with 3 N's = target plant with three neighbor plants).

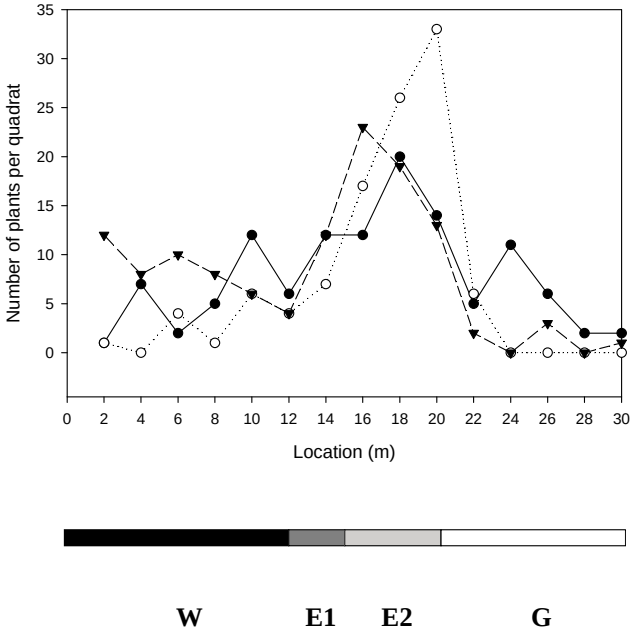


Figure 2. Experimental site survey. Density of naturally occurring plants is shown for 2 m x 1 m quadrats in three transects passing through the habitats (W = woodland; E1 = edge toward woodland side; E2 = edge toward grassland side; G = grassland) (see Figure 1B for transect placement). The definition of edge area depended on vegetation and shade from trees. Edge vegetation changed from small trees/shrubs (E1) to grasses (E2) around the 15-meter mark. The shade line from the woodland trees stayed around the 18-meter mark until mid-morning; later in the day, the edge area was unshaded. The experimental transects were located at approximately 1-2 m (woodland), 13-14 m (edge), and 28-29 m (grassland).

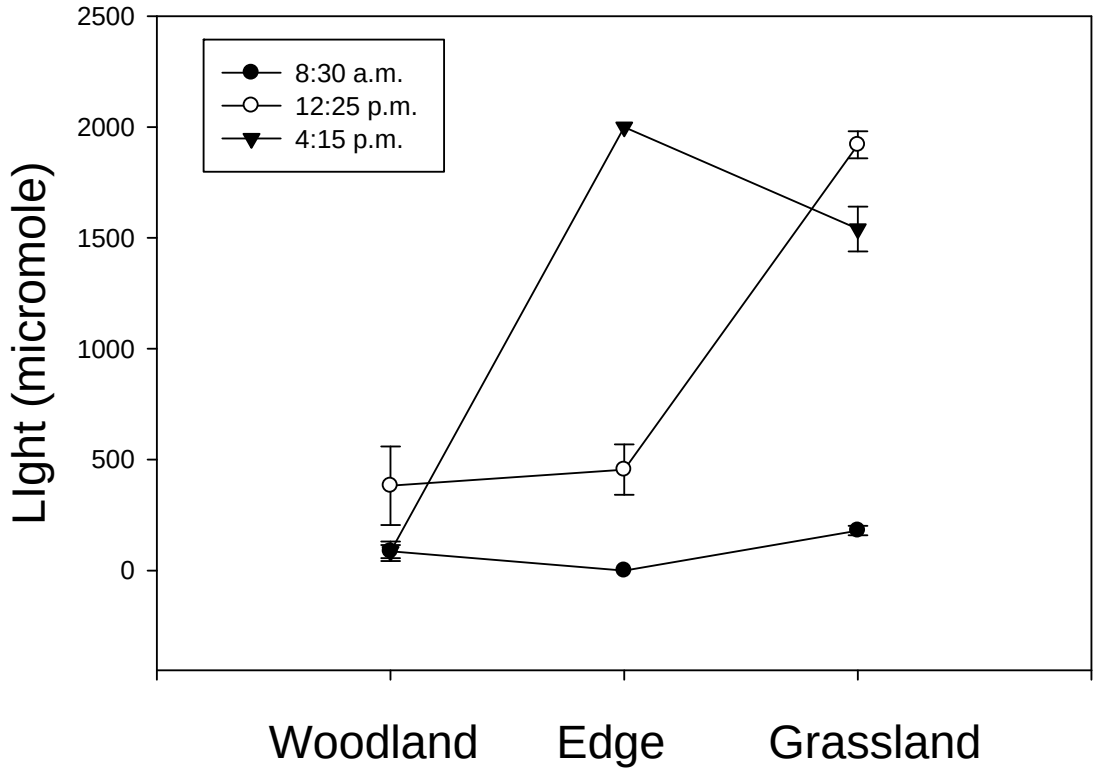
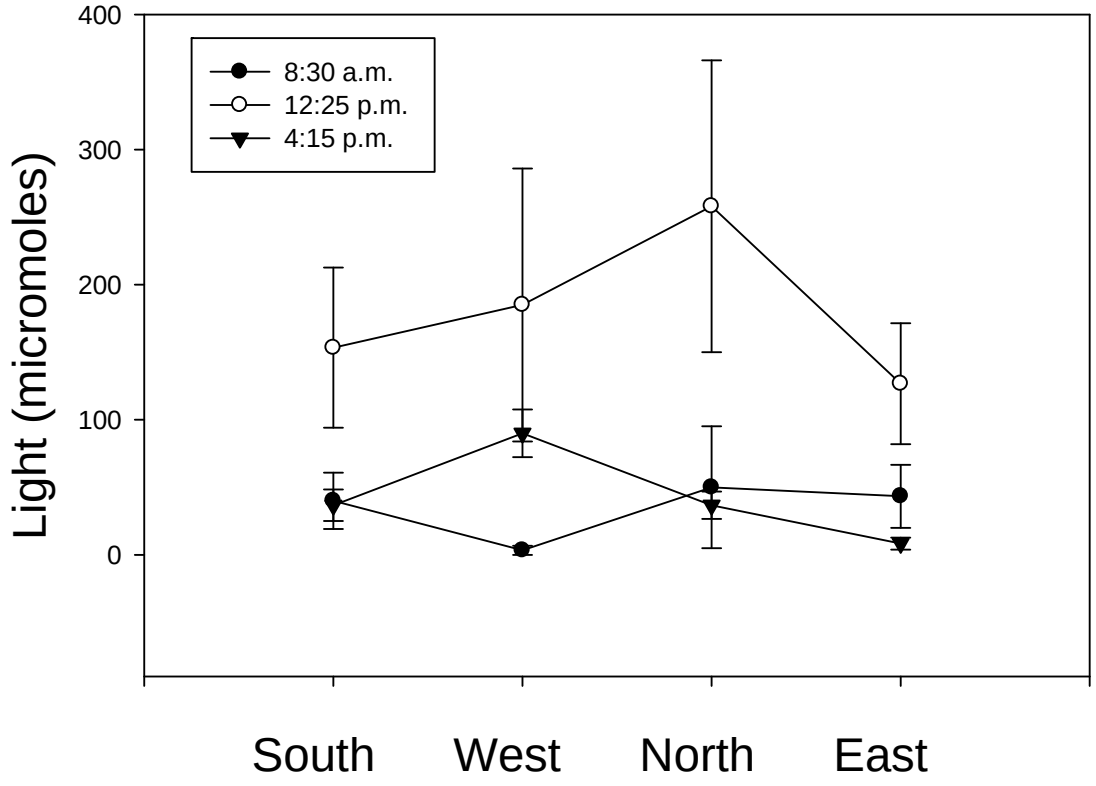
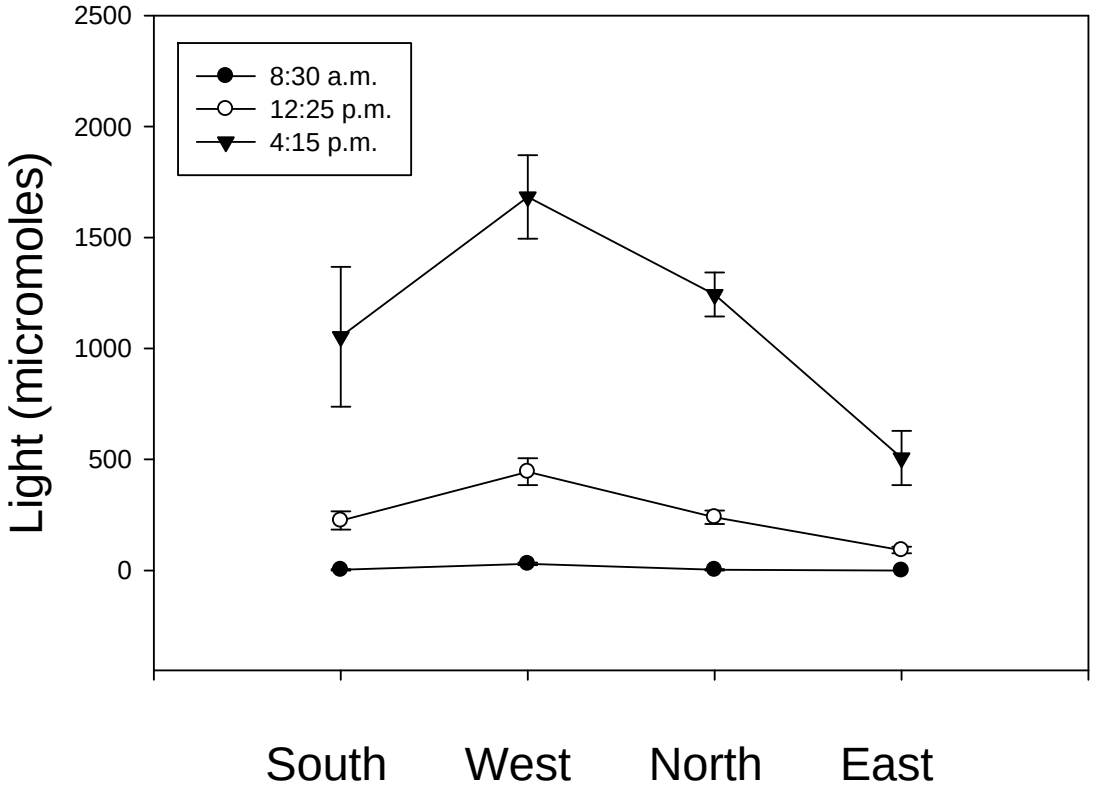


Figure 3. Comparisons of average light levels (± 1 S.E.) for clusters of five experimental plants depending on habitat and time of day. The light meter for each measurement was pointed at the sun. The lines connecting the symbols should not be interpreted as indicating light levels at intermediate locations along the ecotone.

a.


400
300
200
100
0
Light (micromoles)
8:30 a.m.
12:25 p.m.
4:15 p.m.
South
West
North
East

b.


2500
2000
1500
1000
500
0
Light (micromoles)
8:30 a.m.
12:25 p.m.
4:15 p.m.
South
West
North
East

c.

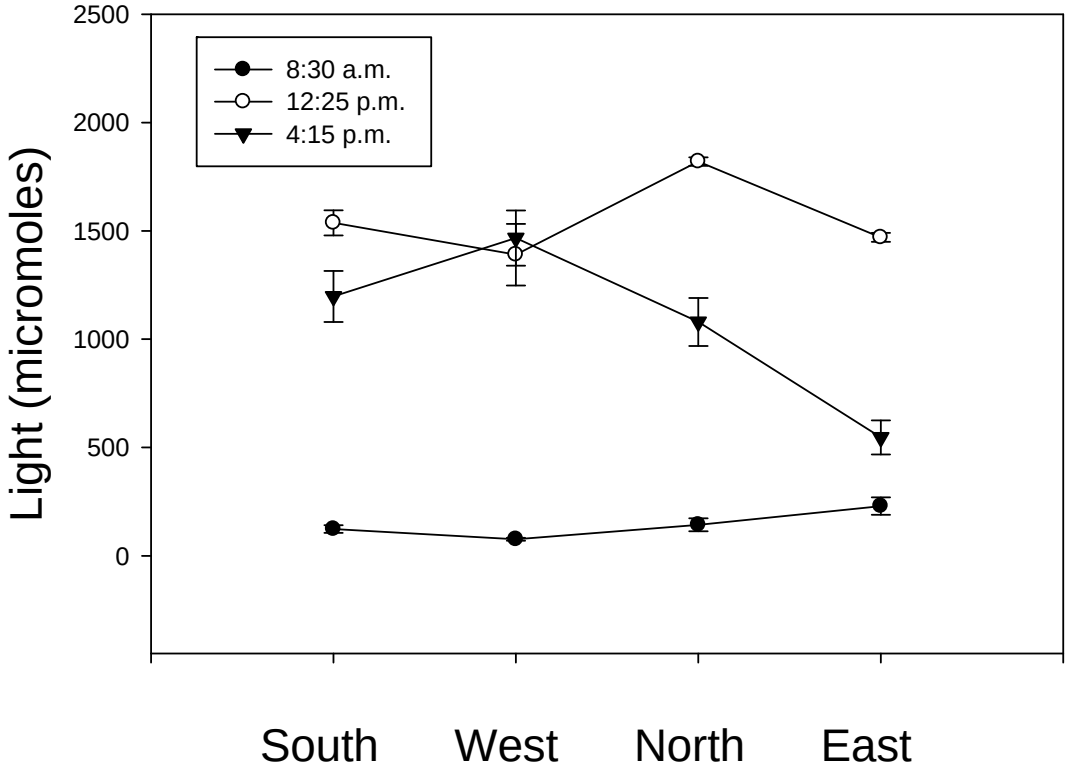
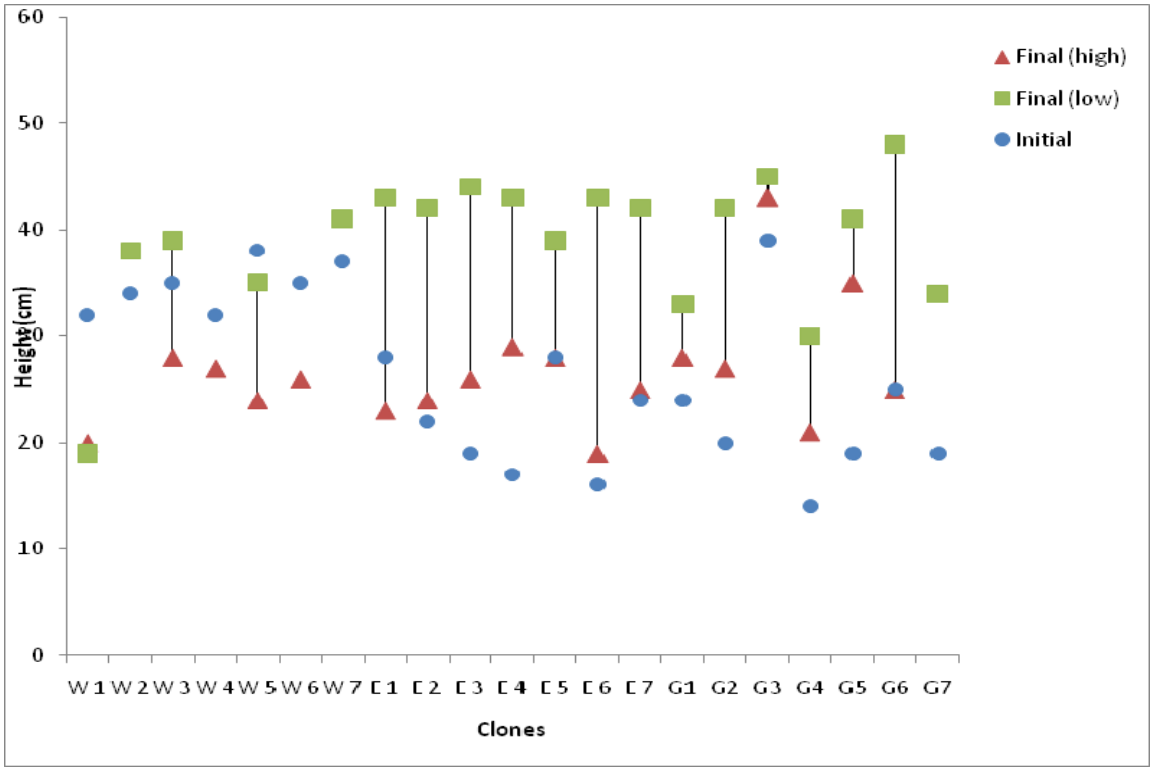


Figure 4. Comparisons of average light levels (± 1 S.E.) for clusters of five experimental plants depending on direction and time of day for the woodland (a), edge (b), and grassland (c) habitat. Note change in Y-axis scaling between graphs. The lines connecting the symbols should not be interpreted as indicating light levels at intermediate locations along the ecotone.

A.


60
50
40
30
20
10
0
Height (cm)
W 1 W 2 W 3 W 4 W 5 W 6 W 7 E 1 E 2 E 3 E 4 E 5 E 6 E 7 G1 G2 G3 G4 G5 G6 G7
Clones
Final (high)
Final (low)
Initial

B.

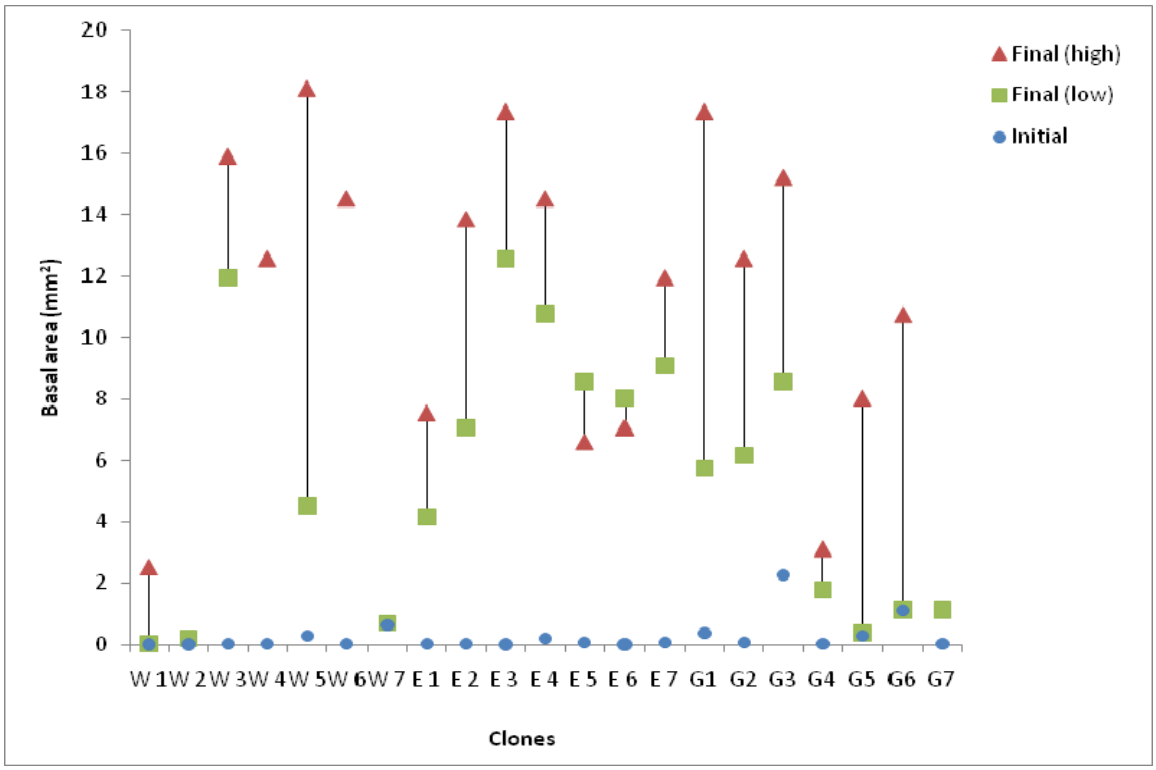

20
18
16
14
12
10
8
6
4
2
0
Basal area (mm²)
W 1 W 2 W 3 W 4 W 5 W 6 W 7 E 1 E 2 E 3 E 4 E 5 E 6 E 7 G1 G2 G3 G4 G5 G6 G7
Clones
Final (high)
Final (low)
Initial

Figure 5. Comparison of clone plant height (A) and basal area (B) under high and low light environments. Original plants were taken from W (woodland), E (edge), and G (grassland) habitats (clones arranged by habitat on X axis). Pairs of clones derived from the same original plant are joined by lines. Initial height and basal area data are included.

Table 1. Comparison of naturally occurring plants in woodland, edge, and grassland habitats. Descriptive statistics are shown in mean(SE)n format. A. Percentage of locations with *C. blanda*, plant density, and plant size measurements in the broad survey. B. Plant size, reproduction, disease, and biomass measurements for border plants (naturally occurring plants adjacent to the experimental transects).

A.

	HABITAT			STATISTICAL SIGNIFICANCE
	WOODLAND	EDGE	GRASSLAND	
BROAD SURVEY				
% locations with plants	39	56	28	X^2=5.83;df=2;p=0.054
Mean density of locations with plants	1.6(0.25)14	2.7(0.36)18	2.4(0.64)10	$F_{2,39}$=2.38;p=0.106;R^2=10.88
Height (cm)	40.36(2.85)14	31.67(2.33)18	31.1(3.82)10	$F_{2,39}$=3.24;p=0.05;R^2=14.23
Basal area (mm^2)	0.81(0.27)14	0.11(0.03)18	0.92(0.64)10	log: $F_{2,39}$=8.73;p=0.001;R^2=30.94

B.

BORDER SURVEY				
May 2007				
Height (cm)	36.93(1.41)28	28.32(1.45)28	30.11(1.75)28	$F_{2,81}$=8.66;p<.001;R^2=17.61
Basal area (mm^2)	0.36(0.09)28	0.13(0.05)28	1.17(0.42)28	log: $F_{2,81}$=10.13;p<.001;R^2=20.01
% reproducing	100	100	93	X^2=4.10;df=2
Seed count	44.04(9.96)28	102.2(35.0)28	76.9(15.5)26	log: $F_{2,79}$=3.12;p=0.049;R^2=7.33
October 2007				
Survival 5/07 to 10/07 (%)	89	79	96	X^2=4.31;df=2;p=0.116
Height (cm)	26.76(1.72)25	18.73(1.97)22	17.41(1.27)27	$F_{2,71}$=9.74;p<.001;R^2=21.53
Basal area (mm^2)	0.38(0.09)25	0.07(0.03)22	0.75(0.38)27	log: $F_{2,71}$=12.05;p<.001;R^2=25.35
June 2008				
Survival 10/07 to 6/08 (%)	79	29	93	X^2=28.71;df=2;p<.001
Height (cm)	35.86(1.88)22	30.75(3.10)8	28.77(1.35)26	$F_{2,53}$=4.81;p=0.012;R^2=15.37
Basal area (cm^2)	0.53(0.13)22	0.04(0.02)8	1.54(0.59)26	log: $F_{2,53}$=6.72;p=0.003;R^2=20.22
% reproducing	100	88	73	X^2=7.08;df=2;p=.029
Seed count	129.9(36.8)22	56.8(29.6)7	229.4(79.1)19	log: $F_{2,45}$=2.43;p=0.100;R^2=9.73
Biomass – aboveground (gm)	5.27(1.12)10	1.93(0.70)8	4.06(1.28)10	log: $F_{2,25}$=3.19;p=0.058;R^2=20.35
Biomass – belowground (gm)	1.34(0.41)10	0.94(0.28)8	9.31(4.95)10	log: $F_{2,25}$=2.28;p=0.123;R^2=15.41

Table 2. Habitat and competition treatment comparisons in the field transplant experiment. Statistical analyses shown are from complex models that included other independent variables and interaction terms; see text and Appendix for details. A significance term of NS indicates that term was dropped from the more complex model. Mean(SE)n shown. W=woodland; E=edge; G=grassland; A=alone; C=competitive

	HABITAT			SIGNIFICANCE	COMPETITION		SIGNIFICANCE
	W	E	G		A	C	
November 2006 data collection							
Height (cm)	27.91(0.82) 53	24.61(0.88) 51	18.04(0.68) 52	$F_{(2,152)}$=52.30; p<.001	22.82(0.74) 81	24.32(0.85) 75	NS
Basal area (mm^2)	2.89(0.45) 53	5.39(1.05) 51	2.88(0.41) 52	$F_{(2,151)}$=9.75; p<.001	5.27(0.71) 81	2.02(0.28) 75	$F_{(1,151)}$=32.81; p<.001
May 2007 data collection							
Height (cm)	36.31(1.40) 48	33.08(1.58) 48	31.42(0.92) 50	$F_{(2,137)}$=5.83; p=0.004	33.92(1.05) 79	33.16(1.15) 67	NS
Basal area (mm^2)	4.25(1.03) 48	7.10(1.17) 48	6.42(1.01) 50	NS	8.47(1.00) 79	2.93(0.44) 67	$F_{(1,141)}$=29.50; p<.001
Seed count	420.9(82.6) 48	627.9(73.8) 48	722.3(80.4) 50	$F_{(2,140)}$=5.38; p=0.006	776.3(73.0) 79	375.1(40.3) 67	$F_{(1,140)}$=32.40; p<.001
July 2008 data collection							
Biomass (aboveground)	0.66(0.22) 9	1.44(0.28) 20	5.42(0.85) 19	log: $F_{(2,45)}$=12.52; p<.001	3.89(0.73) 27	1.56(0.35) 21	$F_{(1,46)}$=6.86; p=0.012
Biomass (belowground)	0.94(0.33) 9	4.68(0.95) 20	4.44(0.83) 19	log: $F_{(2,45)}$=9.42; p<.001	5.32(0.80) 27	2.04(0.50) 21	$F_{(1,46)}$=10.60; p=0.002

Table 3. Comparisons of disease incidence (percentage diseased) for habitat treatments for naturally occurring plants and experimental plants from the field transplant experiment site. Disease incidence in competition treatments for experimental plants is included. Habitat categories were W=woodland, E=edge, and G=grassland; competition treatments were A=alone and C=competitive.

	HABITAT			SIGNIFICANCE	COMPETITION		SIGNIFICANCE
	W	E	G		A	C	
A. Naturally occurring							
Smut % (May 2007)	32	11	0	X^2=12.25;df=2; p=0.002			
Rust % (October 2007)	80	50	33	X^2=11.59;df=2; p=0.003			
B. Experimental							
Rust % (November 2006)	42	33	12	X^2=12.23;df=2; p=0.002	25	63	X^2=6.79;df=1; p=0.009
Smut % (May 2007)	73	46	0	X^2=55.95;df=2; p<.001	39	39	X^2=0.003;df=1; p=0.957
Rust % (November 2007)	73	34	18	X^2=22.94;df=2; p<.001	37	35	X^2=0.041;df=1; p=0.840

Table 4. Results from two-way analyses of variance on light measurements of experimental plants. A. Analysis of effect of time (8:30 a.m., 12:25 p.m., 4:15 p.m.) and habitat (W = woodland, E = edge, and G = grassland) for measurements taken directly at the sun. B. Analyses of effect of time and direction (N, S, E, W) on light measurements. Separate analyses were done for each habitat.

A.

Time	$F_{(2,18)}$=148.56;p<.001
Habitat	$F_{(2,18)}$=118.54:p<.001
Time x Habitat	$F_{(4,18)}$=69.83;p<.001
R^2	97.84

B.

	W	E	G
Time	$F_{(2,24)}$=10.48; p=.001	$F_{(2,24)}$=99.28; p<.001	$F_{(2,24)}$=325.77; p<.001
Direction	$F_{(3,24)}$=.65; p=.591	$F_{(3,24)}$=9.97; p<.001	$F_{(3,24)}$=6.74; p=.002
Time x Direction	$F_{(6,24)}$=.61; p=.718	$F_{(6,24)}$=4.41; p=.004	$F_{(6,24)}$=11.54; p<.001
R^2	52.56	91.40	96.8

Table 5. Comparisons of average height and basal area for growth chamber plants originating from three habitats at field site. Initial measurements are included, as well as results from plants grown under low and high light in the growth chamber. Mean(SE)n shown.

	HABITAT			STATISTICAL SIGNIFICANCE
	WOODLAND	EDGE	GRASSLAND	
INITIAL MEASUREMENTS				
Height (cm)	34.71(0.87)7	22.00(1.86)7	22.86(3.02)7	log: $F_{2,18}$=9.80;p=.001;R^2=52.12
Basal area (mm^2)	0.15(0.09)7	0.06(0.02)7	0.6(0.31)7	log: $F_{2,18}$=2.85;p=0.084;R^2=24.06
FINAL MEASUREMENTS				
Low light height (cm)	31.00(6.11)3	42.29(0.61)7	39.83(2.85)6	$F_{2,13}$=3.65;p=0.055;R^2=35.95
High light height (cm)	24.00(2.31)3	24.86(1.26)7	29.83(3.23)6	$F_{2,13}$=1.65;p=0.231;R^2=20.21
Low light basal area (mm^2)	5.49(3.48)3	8.60(1.01)7	3.95(1.35)6	$F_{2,13}$=2.75;p=0.101;R^2=29.74
High light basal area (mm^2)	12.18(4.86)3	11.27(1.60)7	11.18(2.09)6	$F_{2,13}$=0.04;p=0.962;R^2=0.59

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Appendix table. Plant source, top/bottom, and initial measurement comparisons in the field transplant experiment. Significant interactions are also included. Statistical analyses shown are from complex models with other independent variables and interaction terms; see Table 2 for habitat and competition. If the significance term is listed as NS, that term was dropped from the more complex model. Mean(SE)n shown.

	PLANT SOURCE		STATISTICAL SIGNIFICANCE
	SITE 1	SITE 2	
November 2006 data collection			
Height (cm)	23.56(0.82)81	23.52(0.78)75	NS
Basal area (mm^2)	3.48(0.70)81	3.96(0.39)75	NS
Survival 6/06 to 11/06 (%)	96	89	NS
Rust presence (%)	28	29	NS
May 2007 data collection			
Height (cm)	32.76(1.09)75	34.44(1.10)71	NS
Basal area (mm^2)	5.19(0.90)75	6.71(0.86)71	NS
% reproducing			
Seed count	478.7(57.7)75	712.0(71.5)71	$F_{(1,140)}$=6.52;p=0.012
Survival 11/06 to5/07 (%)	93	95	NS
Smut presence (%)	39	39	NS
November 2007 data collection			
Rust presence (%)	34	38	NS
	TOP/BOTTOM		STATISTICAL SIGNIFICANCE
	TOP	BOTTOM	
November 2006 data collection			
Height (cm)	24.14(0.83)78	22.96(0.76)78	NS
Basal area (mm^2)	3.58(0.68)78	3.83(0.47)78	NS
Survival 6/06 to 11/06 (%)	93	93	NS
Rust presence (%)	37	21	Z=-1.41;p=0.160
May 2007 data collection			
Height (cm)	30.47(1.05)74	36.76(1.02)72	$F_{(1,137)}$=26.58;p<.001
Basal area (mm^2)	6.87(0.98)74	4.96(0.75)72	$F_{(1,141)}$=4.37;p=0.038
% reproducing			
Seed count	634.6(73.1)72	550.9(58.1)74	NS
Survival 11/06 to 5/07 (%)	92	95	NS
Smut presence (%)	46	32	NS
November 2007 data collection			
Rust presence (%)	40	32	NS

	INITIAL MEASUREMENT SIGNIFICANCE
November 2006 data collection	
Height	$F_{(1,152)}$=33.53;p<.001
Basal area	$F_{(1,151)}$=90.78;p<.001
Survival 6/06 to 11/06 (Ht 6/06)	Z=3.86;p<.001
Survival 6/06 to 11/06 (B. area 6/06)	Z=3.28;p=0.001
Rust presence (Ht & B. area 11/06)	NS
May 2007 data collection	
Height	$F_{(1,137)}$=16.44;p<.001
Basal area	$F_{(1,141)}$=26.39;p<.001
Seed count (Ht 6/06)	$F_{(1,140)}$=21.03;p<.001
Seed count (B. area 6/06)	$F_{(1,139)}$=27.97;p<.001
Survival (11/06 to 5/07 – Ht 6/06)	Z=4.49;p<.001
Survival (11/06 to 5/07 – B. area 6/06)	Z=3.73;p<.001
Smut presence (# seeds 5/07)	Z=2.35;p=0.019
November 2007 data collection	
Rust presence (Ht & B. area 11/07)	NS

	INTERACTIONS
November 11/06 data collection	
Rust presence	Hab x T/B: Z=3.49;p<.001 Z=0.00;p=0.997
May 2007 data collection	
Height	Hab x T/B: $F_{(2,137)}$=8.17;p<.001 PS x T/B: $F_{(1,137)}$=4.67;p=0.032
Basal area	T/B x A/C: $F_{(1,141)}$=6.45;p=0.012